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Research Article

Two new saprobic species of *Helicosporium* and *Dictyosporium* and a new host record of *Neohelicomyces guizhouensis* isolated from *Phellodendron amurense* (Rutaceae, Tracheophyta) in China

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Abstract

During a survey of saprobic fungi associated with the medicinal plant *Phellodendron amurense* in Guizhou Province, China, three taxa were isolated and examined. Based on morphological characteristics and multigene phylogenetic analyses, two novel species, *Dictyosporium phellodendri* (Dictyosporiaceae, Pleosporales) and *Helicosporium phellodendri* (Tubeufiaceae, Tubeufiales), are proposed. In addition, *Neohelicomyces guizhouensis* (Tubeufiaceae, Tubeufiales) is reported as a new host record. Detailed morphological descriptions, illustrations and molecular evidence are provided to support the establishment of these taxa.

Key words: Cheirosporous, helicosporous, phylogeny, taxonomy, two new species

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Introduction

Phellodendron amurense (Rutaceae, Tracheophyta), a deciduous plant, is mainly distributed in East Asia. It is rich in alkaloids, flavonoids, triterpenoids, coumarins and other bioactive compounds (Chen et al. 2024). In China, it is renowned as one of the most important traditional Chinese medicine plants, listed in the Chinese Pharmacopoeia (2020 edition) and has been widely used for thousands of years (Xian et al. 2014; Wang et al. 2015; Dulan et al. 2022; Zhang et al. 2024). Medicinal plants are recognised as potential reservoirs for uncovering fungal diversity (Du et al. 2024). Endophytic and pathogenic fungi associated with *P. amurense* have been documented (Cao and Qi 1990; Li 2006; Li et al. 2009, 2018; Wen et al. 2022). However, saprobic fungi occurring on this medicinal host remain poorly explored.

Tubeufiaceae was established by Barr (1979) to accommodate the type genus *Tubeufia* and comprises mainly saprobic taxa inhabiting decaying wood. Members of the family are widely distributed in tropical and subtropical regions (Rossman 1987; Kirk et al. 2001; Lumbsch et al. 2010; Boonmee et al. 2014; Luo et al. 2017; Lu et al. 2018a, b), occurring in both terrestrial wood and aquatic environments (Hyde et al. 2016, 2017; Brahamanage et al. 2017; Chaiwan et al. 2017; Lu et al. 2017a, b, c, 2018a, b; Liu et al. 2018; Hongsanan et al. 2020). Morphologically, members of the family are characterised by helicosporous conidia in the asexual morph (Linder 1929; Samuels and Muller 1979; Spatafora et al. 2006;Tsui et al. 2006; Tsui Barr Lu et al. 2018b; Dong et al. 2020;Zhang et al.2020) and by superficial ascomata, bitunicate asci and hyaline to pale brown, elongate to obovoid, septate ascospores in the sexual morph (Barr 1980; Kodsueb et al. 2006; Boonmee et al. 2011, 2014; Brahamanage et al. 2017; Lu et al. 2018b; Karimi et al. 2025; Sun et al. 2025). Currently, Tubeufiaceae comprises 54 genera (Lu et al. 2018b; Liu et al. 2019a, b, c, d; Wijayawardene et al. 2022; Karimi et al. 2025), amongst which *Helicosporium* and *Neohelicomyces* represent common helicosporous hyphomycetes within the order Tubeufiales (Lu et al. 2018b).

Dictyosporiaceae was introduced by Boonmee et al (2016) to accommodate most cheirosporous hyphomycetous genera, with *Dictyosporium* designated as the type genus. According to Wang et al (2025), the family includes 23 genera and 178 species, excluding one novel species proposed in this study. Members of Dictyosporiaceae are saprobes on plant litter and decaying wood in both terrestrial and aquatic habitats worldwide (Boonmee et al. 2016; Fu et al. 2021; Shen et al. 2022). The type genus *Dictyosporium* is characterised by its cheiroid conidia (Corda 1836).

During a taxonomic survey of saprophytic fungi, associated with *Phellodendron amurense* in Guizhou Province, China, six fresh collections were obtained from the decaying branches in two forests sites. Morphological observations combined with multigene phylogenetic analyses revealed two novel species, *Helicosporium phellodendri* and *Dictyosporium phellodendri* and a new host record, *Neohelicomyces guizhouensis*. Detailed morphological descriptions, illustrations and molecular evidence are provided herein.

Materials and methods

Sample collection, specimen examination and isolation

Fresh specimens were collected from decaying wood of *Phellodendron amurense* in Anshun City and Guiyang City, Guizhou, China, in October 2024. Relevant collection data were recorded in the field. Specimens were examined and observed using a stereomicroscope (SMZ-168, Nikon, Japan). Micromorphological features were observed and photographed with an ECLIPSE Ni compound microscope (Nikon, Tokyo, Japan), equipped with a Canon 90D digital camera. Photoplates were prepared using Adobe Photoshop CC 2019 (Adobe Systems, USA) and Tarosoft® Image Frame Work.

Single spore isolations were performed following the method described by Senanayake et al. (2020). Germinated conidia were transferred on to fresh potato dextrose agar (PDA) plates and incubated in a 25 °C for colony development.

Material deposition

Dried specimens were deposited in the Herbarium of Cryptogams Kunming Institute of Botany, Academia Sinica (HKAS), Kunming, China. Living cultures were deposited in the Guizhou Culture Collection (GZCC), Guizhou, China. New taxa were registered on the Index Fungorum database (Index Fungorum 2025).

DNA extraction, PCR amplification and sequencing

Fresh mycelia were scraped using a sterile toothpick and transferred to 1.5 ml microcentrifuge tube. Genomic DNA was extracted using the Trelief Hi-Pure Fungus Genomic DNA Extraction Kit (Tsingke, China) according to the manufacturer's instructions. Four genetic loci (LSU, ITS, *tef*1-α and *rpb*2) were amplified using the primers LR0R/ LR5 (Vilgalys and Hester 1990), ITS5/ ITS4 (White et al. 1990), EF1-983F/EF1-2218R (Rehner and Buckley 2005) and fRPB2-5F/ fRPB2-7cR (Liu et al. 1999), respectively. PCR amplification was conducted in a 25 µl reaction mixture containing 21 µl of 1.1 × T3 Super PCR Mix (Tsingke Biotech, Chongqing, China), 2 µl of DNA template and 1 µl of each primer. The cycling parameters for LSU, ITS, *tef*1-a and *rpb*2 followed the protocols of Ma et al. (2024b). Purified PCR products were sequenced by Tsingke Biological Engineering Technology and Services Co., China.

Phylogenetic analyses

Sequence quality was verified using BioEdit v. 7.0.5.3 (Hall 1999). Forward and reverse reads were assembled with SeqMan v. 7.0.0 (DNASTAR, Madison, WI, USA; Swindell and Plasterer 1997) and deposited in GenBank. Similar sequences were retrieved using the BLASTn tool in NCBI (https://www.ncbi.nlm.nih.gov/). Reference sequences used for phylogenetic analyses are listed in Tables 1, 2. Each locus was aligned using MAFFT v.7.473 (Katoh et al. 2019) on the online server (https://mafft.cbrc.jp/alignment/server/) and ambiguous regions were trimmed using trimAl v.1.2rev59 (Capella-Gutiérrez et al. 2009). The alignments were concatenated using SequenceMatrix-Windows-1.7.8 (Vaidya et al. 2011).

Maximum Likelihood (ML) analyses were performed with the IQ-TREE web server (http://iqtree.cibiv.univie.ac.at/, Nguyen et al. 2015; Zeng et al. 2023) using default parameters. Bayesian Inference (BI) analyses followed the procedures described by Lu et al (2022). The best-fit substitution model for each gene partition was determined using MrModelTest 2.3 under the Akaike Information Criterion (AIC) (Nylander et al. 2008).

Phylogenetic results

The first phylogenetic tree represents the phylogenetic positions of the new collections within Tubeufiaceae, based on four loci: LSU, ITS, *tef*1-α and *rpb*2. The concatenated dataset comprised 3,411 characters (LSU: 1–851, ITS: 852–1,441, *tef*1-α: 1,442–2,353, *rpb*2: 2,354–3,411), including gaps. A total of 73 strains, including isolates obtained in this study and two outgroups, *Botryosphaeria agaves* (MFLUCC 10-0051) and *B. dothidea* (CBS 115476), were analysed. Both ML and BI analyses yielded similar tree topologies. Fig. 1 illustrates

Table 1. Taxa used for Tubeufiaceae species in this study and their GenBank accession numbers.

Taxon	Strain	GenBank Accession numbers			
		LSU	ITS	*tef*1–α	*rpb*2
Acanthostigma chiangmaiensis	MFLUCC 10-0125^{T}	JN865197	JN865209	KF301560	–
Acanthostigma perpusillum	UAMH 7237	AY856892	AY916492	–	–
Botryosphaeria agaves	MFLUCC 10-0051	JX646807	JX646790	–	–
Botryosphaeria dothidea	CBS 115476	DQ678051	KF766151	DQ767637	DQ677944
Helicosporium acropleurogenum	CGMCC 3.25563^{T}	PP639430	PP626574	PP596333	PP596460
Helicosporium aquaticum	MFLUCC 17-2008^{T}	MH558859	MH558733	MH550924	MH551049
Helicosporium brunneisporum	CGMCC 3.25542^{T}	PP639433	PP626577	PP596336	PP596463
Helicosporium changjiangense	GZCC 22-2113^{T}	PP639434	PP626578	PP596337	PP596464
Helicosporium flavisporum	MFLUCC 17-2020^{T}	MH558860	MH558734	MH550925	MH551050
Helicosporium flavum	MFLUCC 16-1230^{T}	KY873621	KY873626	KY873285	–
Helicosporium hainanense	GZAAS 22-2006^{T}	OP508770	OP508730	OP698081	OP698070
Helicosporium jiangkouense	HKAS 128933^{T}	PP639436	PP626580	PP596339	PP596466
Helicosporium latisporum	HKAS 128960^{T}	PP639437	PP626582	PP596340	PP596467
Helicosporium liuzhouense	GZCC 22-2014^{T}	OQ981402	OQ981394	OQ980476	OQ980474
Helicosporium luteosporum	MFLUCC 16-0226^{T}	KY321327	KY321324	KY792601	MH551056
Helicosporium multidentatum	GZCC 22-2013^{T}	OQ981403	OQ981395	OQ980477	OQ980475
Helicosporium multiseptatum	HKAS_136882^{T}	PQ570860	PQ570843	PQ761135	–
Helicosporium nanningense	GZCC 22-2175^{T}	OR066425	OR066418	OR058864	OR058857
Helicosporium phellodendri	**GZCC 25-0005^{T}**	**PX220124**	**PX220122**	**PX667152**	**PX667156**
Helicosporium phellodendri	**GZCC 25-0006**	**PX220125**	**PX220123**	**PX667153**	**PX667157**
Helicosporium ramosiphorum	CGMCC 3.25541^{T}	PP639432	PP626576	PP596335	PP596462
Helicosporium rubrum	MFLUCC 24-0090^{T}	PQ098514	PQ098477	PQ490681	PQ490675
Helicosporium setiferum	MFLUCC 17-1994^{T}	MH558861	MH558735	MH550926	MH551051
Helicosporium sexuale	MFLUCC 16-1244^{T}	MZ538537	MZ538503	MZ567082	MZ567111
Helicosporium sp.	NBRC 9014	AY856903	AY916489	–	–
Helicosporium thailandense	MFLUCC 18-1407^{T}	MN913718	MT627698	MT954371	–
Helicosporium vegetum	GZCC 23-0060	PP639439	PP626584	PP596342	PP596469
Helicosporium vesicarium	MFLUCC 17-1795^{T}	MH558864	MH558739	MH550930	MH551055
Helicosporium viridiflavum	MFLUCC 17-2336^{T}	–	MH558738	MH550929	MH551054
Helicosporium viridisporum	GZCC 22-2008^{T}	OP508776	OP508736	OP698087	OP698076
Helicotubeufia hydei	MFLUCC 17-1980^{T}	MH290026	MH290021	MH290031	MH290036
Helicotubeufia jonesii	MFLUCC 17-0043^{T}	MH290025	MH290020	MH290030	MH290035
Muripulchra aquatica	MFLUCC 15-0249^{T}	KY320549	KY320532	–	–
Neohelicomyces acropleurogenus	CGMCC 3.25549^{T}	PP639450	PP626594	PP596351	PP596478
Neohelicomyces aquaticus	MFLUCC 16-0993^{T}	KY320545	KY320528	KY320561	MH551066
Neohelicomyces aseptatus	CGMCC 3.25564^{T}	PP639451	PP626595	PP596352	PP596479
Neohelicomyces dehongensis	MFLUCC 18-1029^{T}	MN913709	NR_171880	MT954393	–
Neohelicomyces denticulatus	GZCC 19-0444^{T}	MW133855	OP377832	–	–
Neohelicomyces deschampsiae	CPC 33686^{T}	MK442538	MK442602	–	–
Neohelicomyces edgeworthiae	CGMCC 3.25565^{T}	PP639453	PP626597	PP596354	PP596481
Neohelicomyces grandisporus	KUMCC 15-0470^{T}	KX454174	KX454173	–	MH551067
Neohelicomyces guizhouensis	GZCC 23-0725^{T}	PP512973	PP512969	PP526727	PP526733
Neohelicomyces guizhouensis	**GZCC 25-0007**	**PX645246**	**PX649070**	**PX667150**	**PX667154**

Taxon	Strain	GenBank Accession numbers			
		LSU	ITS	*tef*1–α	*rpb*2
Neohelicomyces guizhouensis	**GZCC 25-0008**	**PX645247**	**PX649071**	**PX667151**	**PX667155**
Neohelicomyces guttulatus	CGMCC 3.25550[T]	PP639454	PP626598	PP596355	–
Neohelicomyces hainanensis	GZCC 22-2009[T]	OP508774	OP508734	OP698085	OP698074
Neohelicomyces helicosporus	GZCC 23-0633[T]	PP512975	PP512971	PP526729	PP526735
Neohelicomyces hyalosporus	GZCC 16-0086[T]	MH558870	MH558745	MH550936	MH551064
Neohelicomyces hydei	GZCC 23-0727[T]	PP512977	–	PP526731	PP526737
Neohelicomyces lignicola	CGMCC 3.25551[T]	PP639456	PP626600	PP596357	PP596483
Neohelicomyces longisetosus	NCYU-106H1-1-1[T]	–	MT939303	–	–
Neohelicomyces macrosporus	CGMCC 3.25552[T]	PP639457	PP626601	PP596358	PP596484
Neohelicomyces maolanensis	GZCC 23-0079[T]	PQ098529	–	PQ490683	PQ490677
Neohelicomyces melaleucae	CPC 38042[T]	MN567661	MN562154	MN556835	–
Neohelicomyces pallidus	CBS 271.52	AY856887	AY916461	–	–
Neohelicomyces pallidus	CBS 962.69	AY856886	AY916460	–	–
Neohelicomyces pandanicola	KUMCC 16-0143[T]	MH260307	MH275073	MH412779	–
Neohelicomyces qixingyaensis	CGMCC 3.25569[T]	PP639458	PP626602	PP596359	PP596485
Neohelicomyces submersus	MFLUCC 16-1106[T]	KY320547	KY320530	–	MH551068
Neohelicomyces subtropicus	GZCC 23-0076[T]	PQ098530	PQ098492	PQ490685	PQ490679
Neohelicomyces thailandicus	MFLUCC 11-0005[T]	MN913696	NR_171882		–
Neohelicomyces xiayadongensis	CGMCC 3.25568[T]	PP639460	PP626604	PP596361	PP596487
Neohelicomyces yunnanensis	GZCC 23-0735[T]	PP664113	PP664109	–	–
Tubeufia guttulata	GZCC 23-0404[T]	OR030834	OR030841	OR046678	OR046684
Tubeufia hainanensis	GZCC 22-2015[T]	OR030835	OR030842	OR046679	OR046685
Tubeufia javanica	MFLUCC 12-0545[T]	KJ880036	KJ880034	KJ880037	–
Tubeufia krabiensis	MFLUCC 16-0228[T]	MH558917	MH558792	MH550985	MH551118
Tubeufia latispora	MFLUCC 16-0027[T]	KY092412	KY092417	KY117033	MH551119
Tubeufia laxispora	MFLUCC 16-0232[T]	KY092408	KY092413	KY117029	MF535287
Tubeufia mackenziei	MFLUCC 16-0222[T]	KY092410	KY092415	KY117031	MF535288
Tubeufia muriformis	GZCC 22-2039[T]	OR030836	OR030843	OR046680	OR046686
Tubeufia nigroseptum	CGMCC 3.20430[T]	MZ853187	MZ092716	OM022002	OM022001
Tubeufia pandanicola	MFLUCC 16-0321[T]	MH260325	MH275091	OP698085	OP698074

Note: Newly-generated sequences are shown in bold. A dash ("–") indicates data unavailable in GenBank and "[T]" denotes an ex-type strain.

the best- scoring ML tree, with a final likelihood value of -29709.023. In our phylogenetic tree (Fig. 1), our strains (GZCC 25-0007 and GZCC 25-0008) clustered within *Neohelicomyces*, while GZCC 25-0005 and GZCC 25-0006 clustered within *Helicosporium* in the family Tubeufiaceae.

Phylogenetic analysis of *Dictyosporium* was based on three loci: LSU, ITS and *tef*1-α. The dataset comprised a total of 51 strains, which included isolates obtained in this study as well as the two outgroup taxa, *Aquadictyospora clematidis* (MFLUCC 17-2080) and *A. lignicola* (MFLUCC 17-1318). The concatenated sequence matrix contains 2,352 characters (LSU: 1–851, ITS: 852–1,442, *tef*1-α: 1,443–2,352) including gaps. The phylogenetic tree (Fig. 2) reveals that GZCC 25-0522 and GZCC 25-0523 cluster together with maximal support values (ML/PP = 100/1), forming a distinct and well-supported monophyletic lineage within *Dictyosporium*.

Table 2. Taxa of Dictyosporiaceae used in this study and their GenBank accession numbers.

Taxon	Strain	GenBank Accession numbers		
		LSU	ITS	*tef*1–α
Aquadictyospora clematidis	MFLUCC 17-2080	MT214545	MT310592	MT394727
Aquadictyospora lignicola	MFLUCC 17-1318	MF948629	MF948621	MF953164
Dictyosporium alatum	ATCC 34953^{T}	DQ018101	NR_077171	–
Dictyosporium appendiculatum	MFLUCC 17-2259^{T}	MH376715	MH388343	–
Dictyosporium aquaticum	MF1318^{T}	–	KM610236	–
Dictyosporium australiense	HKUCC 8797	–	DQ018092	–
Dictyosporium bulbosum	yone221	AB807511	LC014544	AB808487
Dictyosporium cycadicola	HUEST 24.0140	PP740388	PP740382	PP776570
Dictyosporium digitatum	KH 401	AB807515	LC014545	AB808491
Dictyosporium digitatum	yone 280	AB807512	LC014547	AB808488
Dictyosporium duliujiangense	KUNCC 23-15949	PQ309046	PQ309055	PQ346450
Dictyosporium duliujiangense	GZCC 19-0426^{T}	MW133815	OQ842725	OQ850746
Dictyosporium elegans	FMR 13125	KY853501	KY853441	–
Dictyosporium elegans	NBRC 32502^{T}	DQ018100	DQ018087	–
Dictyosporium giganticum	BCC 11346	–	DQ018095	–
Dictyosporium guangdongense	ZHKUCC 24-0002^{T}	PP326213	PP326190	–
Dictyosporium guttulatum	MFLUCC 1- 0258^{T}	MH376717	MH388345	MH388379
Dictyosporium heptasporum	CBS 396.59	–	DQ018090	–
Dictyosporium hongkongensis	KUMCC 17-0268	MH376718	MH388346	MH388380
Dictyosporium hughesii	K 1847	AB807517	LC014548	AB808493
Dictyosporium hughesii	KUNCC 23-15923	PQ309047	PQ309056	–
Dictyosporium krabiense	MFLU 16-1890^{T}	MH376719	–	MH388381
Dictyosporium licualae	SNC182	–	PP594915	PP740420
Dictyosporium meiosporum	MFLUCC 10-0131^{T}	KP710945	KP710944	–
Dictyosporium muriformis	GZCC 20-0006^{T}	MN897834	MT002304	MT023011
Dictyosporium nigroapice	MFLUCC 17-2053^{T}	MH381777	MH381768	MH388821
Dictyosporium nigroapice	BCC 3555	–	DQ018085	–
Dictyosporium olivaceosporum	KH 375^{T}	AB807514	LC014542	AB808490
Dictyosporium palmae	CBS-H 22129	KX555648	–	–
Dictyosporium pandanicola	MFLU 16-1886^{T}	MH376720	MH388347	MH388382
Dictyosporium phellodendri	**GZCC 25-0522^{T}**	**PV910482**	**PV916337**	**PX667148**
Dictyosporium phellodendri	**GZCC 25-0523**	**PV910483**	**PV916338**	**PX667149**
Dictyosporium sexualis	MFLUCC 10-0127^{T}	KU179106	KU179105	–
Dictyosporium sp.	J15	–	PP033644	–
Dictyosporium sp.	J16	–	PP033645	–
Dictyosporium sp.	KT 2025	–	MZ359876	–
Dictyosporium sp.	MFLUCC 15-0629	MH381775	MH381766	MH388819
Dictyosporium sp.	19VA07	–	JX270548	–
Dictyosporium fluminicola	KUNCC 23-17212	PQ226144	PQ038338	PQ227066
Dictyosporium stellatum	CCFC 241241^{T}	JF951177	–	–
Dictyosporium strelitziae	CBS 123359^{T}	FJ839653	–	–
Dictyosporium tetrasporum	K 2865	AB807519	LC014551	AB808495
Dictyosporium thailandicum	MFLUCC 13-0773^{T}	KP716707	KP716706	–
Dictyosporium toruloides	CBS 209.65	DQ018104	DQ018093	–
Dictyosporium tratense	MFLUCC 17-2052^{T}	MH381776	MH381767	MH388820
Dictyosporium tubulatum	MFLUCC 17-2056	MH381779	MH381770	–
Dictyosporium tubulatum	MFLUCC 15-0631^{T}	MH381778	MH381769	MH388822
Dictyosporium variabilisporum	ZHKUCC 24-0003^{T}	PP326215	PP326192	PP333112
Dictyosporium wuyiense	CGMCC 3.18703^{T}	–	KY072977	–
Dictyosporium zhejiangense	HKAS 136886	PQ569961	PQ324184	–
Dictyosporium zhejiangense	MW–2009a^{T}	–	FJ456893	–

Note: Newly-generated sequences are shown in bold. A dash ("–") indicates data unavailable in GenBank and "T" denotes an ex-type strain.

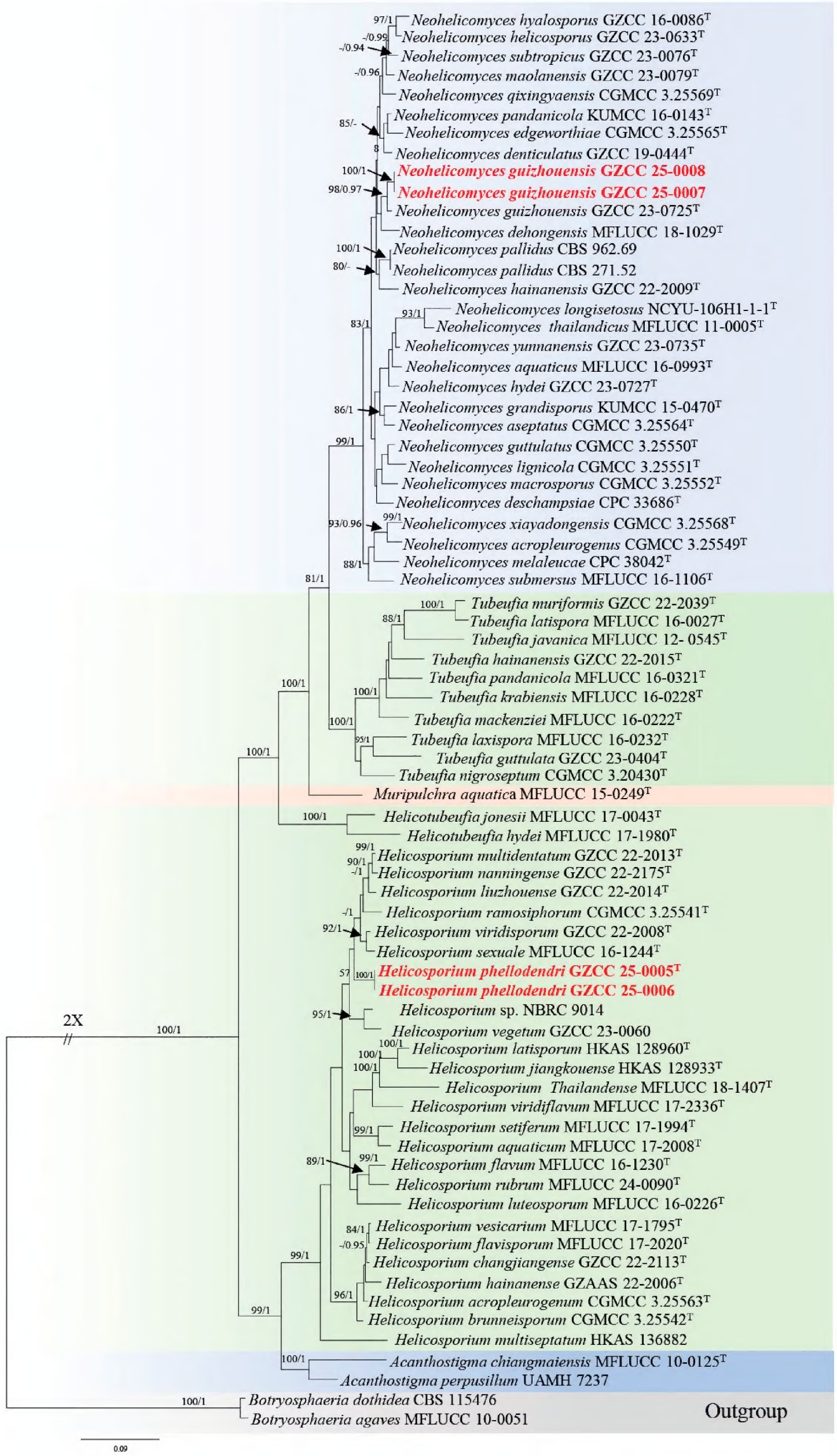

Figure 1. Maximum Likelihood (ML) phylogenetic tree, based on the combined dataset of LSU, ITS, *tef*1-α and *rpb*2 sequences. Bootstrap support values for ML analysis (≥ 75%) and posterior probability (PP) values from Bayesian inference (≥ 0.95) are shown at the corresponding nodes. Ex-type strains are indicated by "T" and newly-generated isolates are highlighted in bold red.

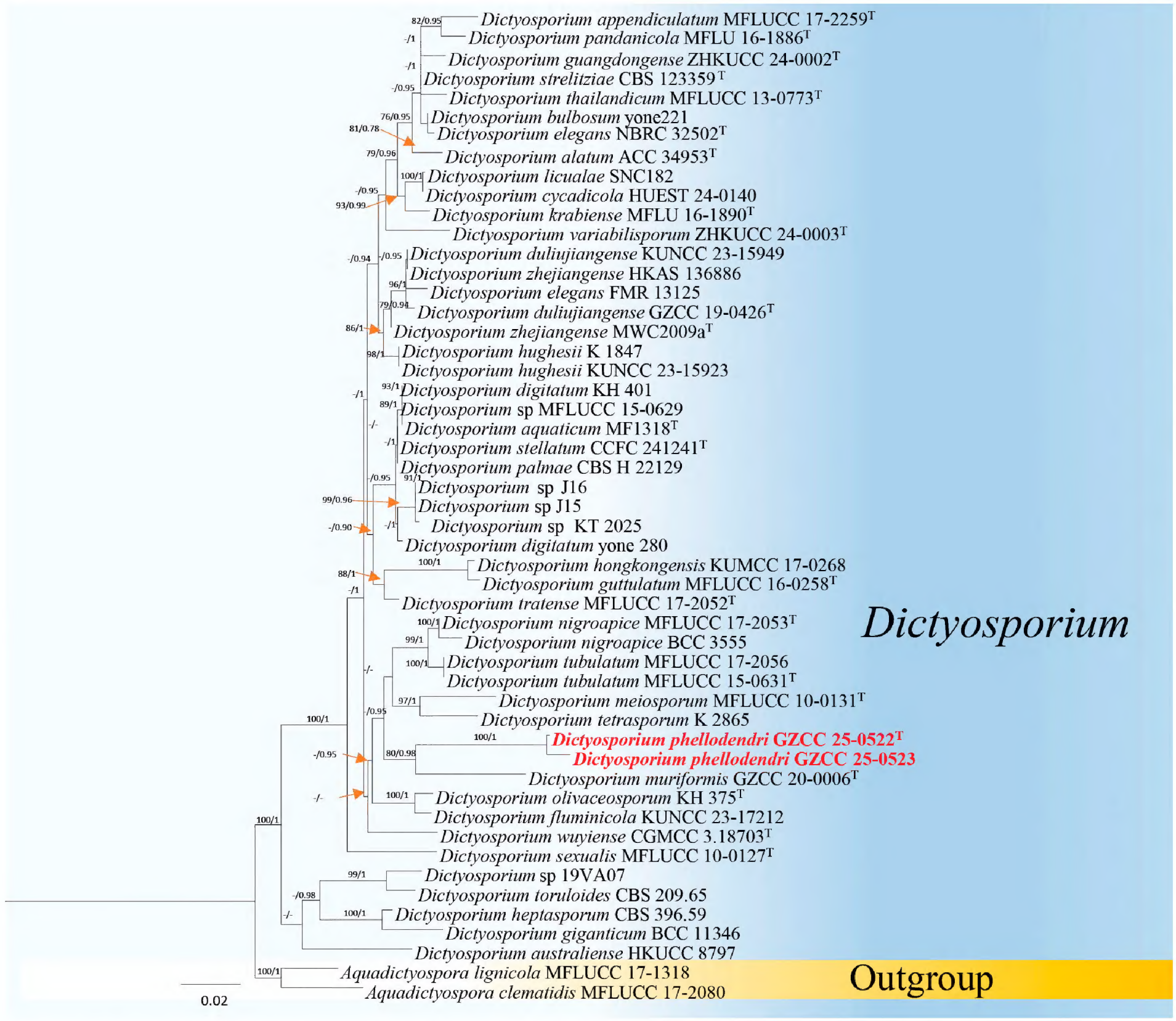

Figure 2. Maximum Likelihood (ML) phylogenetic tree, based on the combined dataset of LSU, ITS and *tef*1-α sequences. Bootstrap support values for ML analysis (≥ 75%) and posterior probability (PP) values from Bayesian inference (≥ 0.95) are shown at the corresponding nodes. Ex-type strains are indicated by "T" and newly-generated isolates are highlighted in bold red.

Taxonomy

***Helicosporium* Nees, Syst. Pilze (Würzburg): 68 (1816) [1816–17]**

Notes. *Helicosporium*, one of the three earliest described helicosporous genera (*Helicoma*, *Helicomyces* and *Helicosporium*) (Link 1809; Nees 1817; Corda 1837), was established by Nees (1817) with *H. vegetum* as the type species. To date, 118 species are recorded in the Index Fungorum (2025). However, based on combined morphological and molecular evidence, only about 32 species are currently accepted in this genus (Lu et al. 2018b; Xiao et al. 2023; Ma et al. 2024b; Bai et al. 2025; Peng et al. 2025; Sun et al. 2025). Amongst these, sexual morphs have been confirmed for only five species: *H. flavum*, *H. sexuale*, *H. vegetum*, *H. rubrum* and *H. multiseptatum* (Boonmee et al. 2014, 2021; Brahmanage et al. 2017; Peng et al. 2025; Sun et al. 2025). Most species of *Helicosporium* are saprobes inhabiting freshwater and terrestrial environments,

with a broad geographical distribution (Morgan-Jones and Goos 1992; Zhao et al. 2007; Lu et al. 2017a, 2018b, 2022; Dong et al. 2020; Boonmee et al. 2021; Hsieh et al. 2021; Xiao et al. 2023; Ma et al. 2024b). The majority of *Helicosporium* species have been isolated from decaying wood of unidentified plant hosts, while *H. multiseptatum* as the saprobe and *H. thailandicum* as the pathogen obtained from Poaceae sp. and *Elaeis* sp. (Arecaceae), respectively (Sun et al. 2025). In this study, we introduce a new *Helicosporium* species which was isolated from medicinal plants.

Helicosporium phellodendri **S.P. Zou, Y. P. Xiao & Y.Z. Lu, sp. nov.**

Index Fungorum: IF904507

Fig. 3

Etymology. the specific epithet "*phellodendri*" refers to the host genus name "*Phellodendron*" from which the fungus was isolated.

Holotype. HKAS 145879.

Description. *Saprobic* on dead wood of *Phellodendron amurense*. ***Sexual morph*** Undetermined. ***Asexual morph*** Hyphomycetous, helicosporous. ***Colonies*** on natural substrate superficial, effuse, gregarious, with masses of crowded, glistening conidia, yellowish-green. ***Mycelium*** partly immersed, partly superficial, composed of pale brown to brown, branched, septate, guttulate, smooth hyphae. ***Conidiophores*** 89–97 × 4–5 µm ($\bar{x}$ = 94 × 4.5 µm, n = 20), macronematous, mononematous, erect, cylindrical, straight or broadly curved, simple or occasionally branched, septate, brown at base, paler towards the apex, thick-walled. ***Conidiogenous cells*** 9.5–10.5 × 3.5–4.8 µm ($\bar{x}$ = 10 × 4.3 µm, n = 15), holoblastic, monoblastic, integrated, intercalary, cylindrical, pale brown to brown, smooth-walled. ***Conidia*** solitary, pleurogenous, helicoid, tapering towards the ends, 10.5–12.5 µm diam. and conidial filament 1.5–2 µm wide ($\bar{x}$ = 11.5 × 1.8 µm, n = 25), 60–65 µm long ($\bar{x}$ = 63 µm, n = 25), tightly coiled 2½–3 times, not becoming loose in water, multi-septate, hyaline, smooth-walled.

Culture characteristics. Conidia produce germ tubes on PDA within 14 hours of incubation at 25 °C. Colonies on PDA are circular, with a flat surface and entire edge, reaching a diameter of 26 mm after 36 days of incubation at 25 °C. The colony appears dark brown to black at centre, brown at outer ring on the top view and brown on the reverse view.

Material examined. CHINA • Guizhou Province, Guiyang City, Qingzhen City, Maige Miao and Bouyei Ethnic Township, Xiaochong Village, 26°74'N, 106°37'E, on the rotting wood of *Phellodendron amurense*, 1 October 2024, Shi-Ping Zou, HB-Z17-1 (HKAS 145879, holotype), ex-type culture GZCC 25-0005 • *Ibid*., HB-Z17-2 (HKAS 145878), living culture GZCC 25-0006.

Notes. Morphological examination indicated that *Helicosporium phellodendri* conforms to the generic concept of *Helicosporium*, characterised by pale yellow to yellow-green colonies on the natural woody substratum, erect setiferous cylindrical conidiophores with denticulate conidiogenous cells and hyaline to yellow-green helicoid conidia which are mainly becoming loosely coiled in water (Ma et al. 2024b). *Helicosporium phellodendri* is morphologically similar to *H. multidentatum*, but differs in having longer conidia (105–130 µm vs. 60–65 µm), with more coils (3¼–3¾ vs. 2½–3). Furthermore, the conidia of *H. multidentatum* become

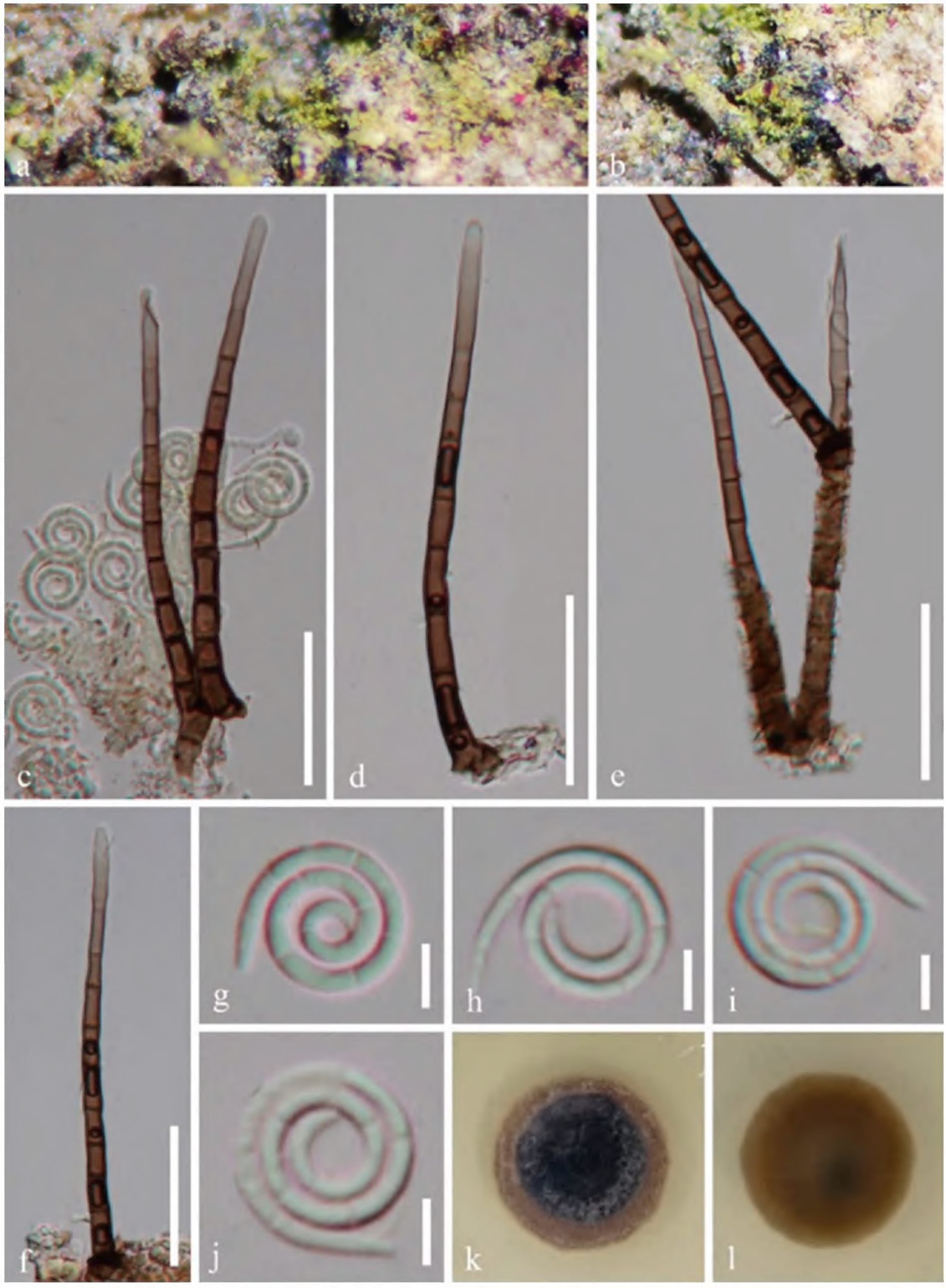

Figure 3. *Helicosporium phellodendri* (HKAS 145879, holotype). **a, b.** Colonies on the natural substrate; **c–f.** Conidiophores and conidiogenous cells; **g–j.** Conidia; **k, l.** Surface and reverse view of colonies on PDA after 36 days of incubation at 25 °C. Scale bars: 30 μm (**c–f**); 5 μm (**g–j**).

loosely coiled in water, while those of *H. phellodendri* do not loosen (Xiao et al. 2023). Phylogenetic analysis (Fig. 1) also supports that *H. phellodendri* and *H. multidentatum* are distinct species. Strains GZCC 25-0005 and GZCC 25-0006 formed a well-supported, independent lineage within *Helicosporium* (Fig. 1). *Helicosporium viridisporum and H. sexuale* are closely related to *H. phellodendri.* However, *H. viridisporum* can be distinguished from *H. phellodendri* by its longer conidiophores (69–189 × 3–5 µm vs. 89–97 × 4–5 µm), denticulate conidiogenous cells and acropleurogenous, aseptate conidia (Lu et al. 2022). *Helicosporium sexuale* displays sexual morph (Boonmee et al. 2021), whereas, *H. phellodendri* exhibits asexual morph. Therefore, *H. phellodendri* is introduced here as a novel species.

Neohelicomyces **Z.L. Luo, Bhat & K.D. Hyde, Cryptog. Mycol. 38(1): 39 (2017)**

Notes. *Neohelicomyces* was proposed by Luo et al. (2017) with *N. aquaticus* designated as the type species. To date, 30 species have been recorded in Index Fungorum (2025). All known taxa represent asexual morphs (Ma et al. 2024a, b), except for *N. sexualis*, which was characterised and linked to its sexual morph, based on both morphological and molecular evidence (Sun et al. 2025). The asexual morphs of *Neohelicomyces* species are characterised by macronematous, mononematous, erect, septate conidiophores with holoblastic conidiogenous cells and loosely or tightly coiled helicoid conidia (Hsieh et al. 2021; Lu et al. 2022; Yang et al. 2023; Ma et al. 2024a, b). In contrast, the sexual morph produces scattered, superficial, solitary, subglobose, light brown ascomata on natural substrates, lacking setae. Ascospores are multiseriate, narrowly cylindrical, straight to slightly curved, hyaline to pale brown, septate and rough (Sun et al. 2025). Species of *Neohelicomyces* are saprobic, typically inhabiting freshwater or terrestrial environments on decaying wood in Asia, Europe and North America, including records from China, Germany and Thailand (Ma et al. 2024a; Sun et al. 2025). Only a few host plants have been documented for this genus (Ma et al. 2024a).

Neohelicomyces guizhouensis **J. Ma, Y.Z. Lu & K.D. Hyde, MycoKeys 105: 323 (2024)**

MycoBank No: 901915

Fig. 4

Description. *Saprobic* on dead wood of *Phellodendron amurense*. ***Sexual morph*** Undetermined. ***Asexual morph*** Hyphomycetous, helicosporous. ***Colonies*** on natural substrate superficial, effuse, gregarious, with mass of crowded conidia, white. ***Mycelium*** partly immersed, partly superficial, composed of hyaline to pale brown, branched, septate, guttulate, smooth hyphae. ***Conidiophores*** 154–175 × 4–5 µm ($\bar{x}$ = 161 × 4.5 µm, n = 20), macronematous, mononematous, erect, cylindrical, tapering towards the apex, straight or slightly flexuous, unbranched, septate, subhyaline to pale brown, thick-walled. ***Conidiogenous cells*** 11–19 × 2.5–4 µm ($\bar{x}$ = 14.5 × 3.5 µm, n = 20), holoblastic, monoblastic or polyblastic, integrated, terminal or intercalary, cylindrical, with denticles, subhyaline to pale brown, smooth-walled. ***Conidia*** solitary, acropleurogenous, helicoid, developing

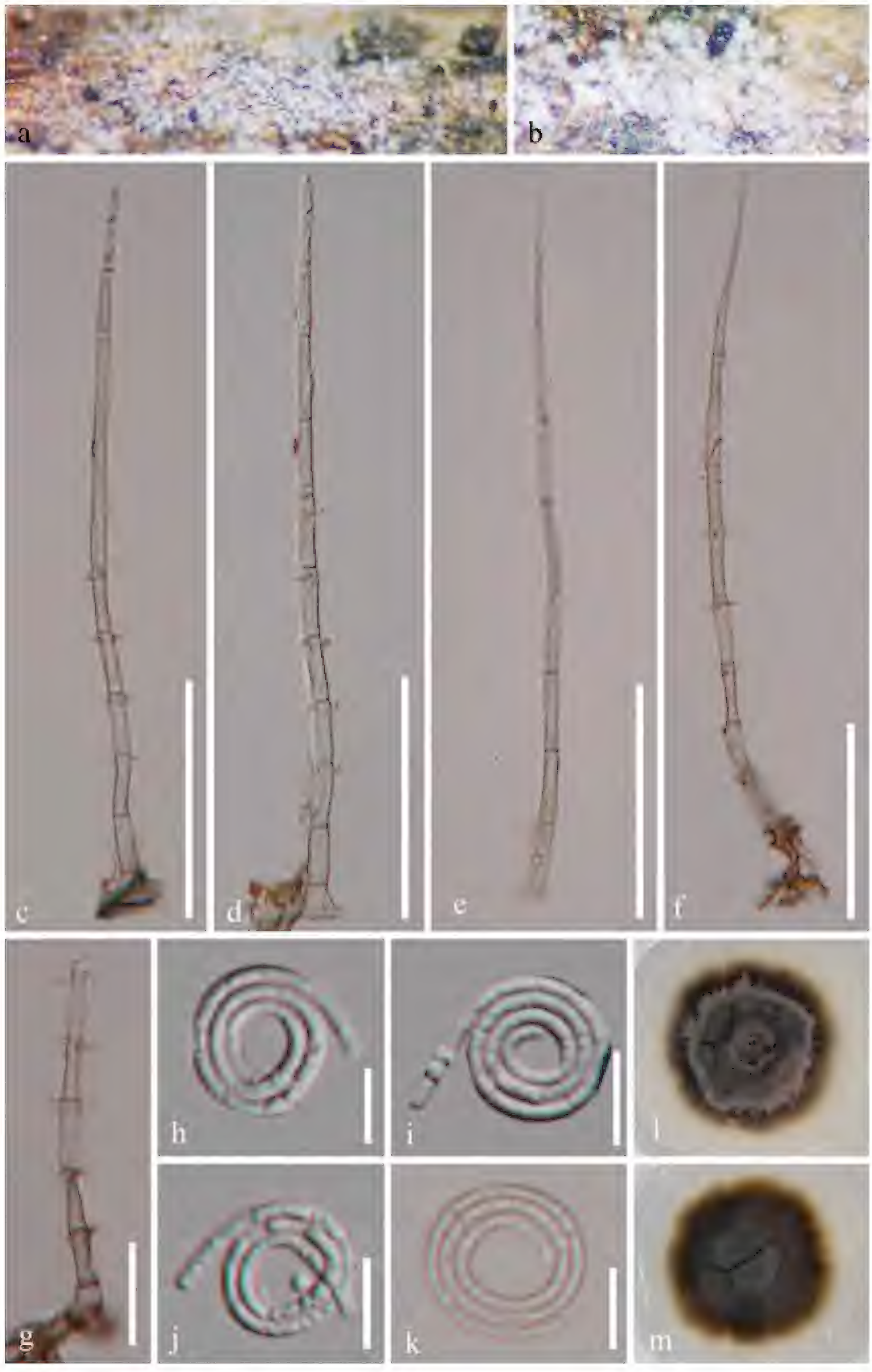

Figure 4. *Neohelicomyces guizhouensis* (HKAS 145881). **a, b.** Colonies on the natural substrate; **c–g.** Conidiophores; **h–k.** Conidia; **l, m.** Surface and reverse view of colonies on PDA after 45 days of incubation at 25 °C. Scale bars: 50 μm (**c–f**); 20 μm (**g**); 10 μm (**h–k**).

on tooth-like protrusion, 14–20 µm diam. and conidial filament 1.5–3 µm wide ($\bar{x}$ = 16 × 2 µm, n = 20), 94–133 µm long ($\bar{x}$ = 113 µm, n = 25), tightly coiled 3–3½ times, not becoming loose in water, guttulate, hyaline, smooth-walled.

Culture characteristics. Conidia produce germ tubes on PDA within 10 hours of incubation at 25 °C. Colonies on PDA are circular, with a raised centre and undulate edge, reaching a diameter of 30 mm after 45 days of incubation at 25 °C. The colony appears grey to pale brown on the top view, with the reverse side ranging from pale brown to brown.

Material examined. CHINA • Guizhou Province, Guiyang City, Qingzhen City, Maige Miao and Bouyei Ethnic Township, Xiaochong Village, 26°74'N, 106°37'E, on the rotting branch of *Phellodendron amurense*, 1 October 2024, Shi-Ping Zou, HB-Z15-1 (HKAS 145881), living culture GZCC 25-0007 • *Ibid*., HB-Z15-2 (HKAS 145880), living culture GZCC 25-0008.

Notes. Phylogenetic analysis showed that our isolates (GZCC 25-0007 and GZCC 25-0008) grouped with *N. guizhouensis* (GZCC 23-0725) by strong support (ML/PP = 98%/0.97; Fig. 1). Pairwise comparison of the ITS, LSU, *tef*1-α and *rpb*2 sequences between GZCC 25-0007 and *N. guizhouensis* (GZCC 23-0725) revealed minimal nucleotide differences: 5 bp/424 bp (1.2%, including two gaps), 3 bp/859 bp (0.3%, including two gaps), 2 bp/892 bp (0.2%, no gaps) and 2 bp/903 bp (0.2%, no gaps), respectively. Morphologically, our new collections share identical characteristics of conidiogenous cells and conidia with the holotype of *N. guizhouensis* (Ma et al. 2024a). Therefore, GZCC 25-0007 and GZCC 25-0008 are identified as *N. guizhouensis*. *Neohelicomyces guizhouensis* was originally described by Ma et al. (2024a) from submerged wood in a stream in China and our study represents its first record associated with *Phellodendron amurense*.

Dictyosporium Corda, Weitenweber's Beitr. Nat. 1: 87 (1837)

Notes. *Dictyosporium* was proposed by Corda (1836) with *D. elegans* designated as the type species. Species of *Dictyosporium* are distributed across the globe in both freshwater and terrestrial habitats, functioning as saprobes and frequently found on decaying wood, plant litter,and in soil (Van Emden 1975; Boonmee et al. 2016; Yang et al. 2018; Zhang et al. 2023). To date, a total of 91 species has been recorded within this genus (Index Fungorum 2025).

Dictyosporium phellodendri S.P. Zou, Y. P. Xiao & Y.Z. Lu, sp. nov.

Index Fungorum: IF904506

Fig. 5

Etymology. The specific epithet "*phellodendri*" refers to the host genus name "*Phellodendron*" from which the fungus was isolated.

Holotype. HKAS 149888.

Description. *Saprobic* on dead wood of *Phellodendron amurense*. ***Sexual morph*** Undetermined. ***Asexual morph*** Hyphomycetous. *Colonies* on natural substrate forming sporodochial conidiomata, superficial, punctiform, scattered, black, glistening. ***Mycelium*** immersed, pale to brown. ***Conidiophores***

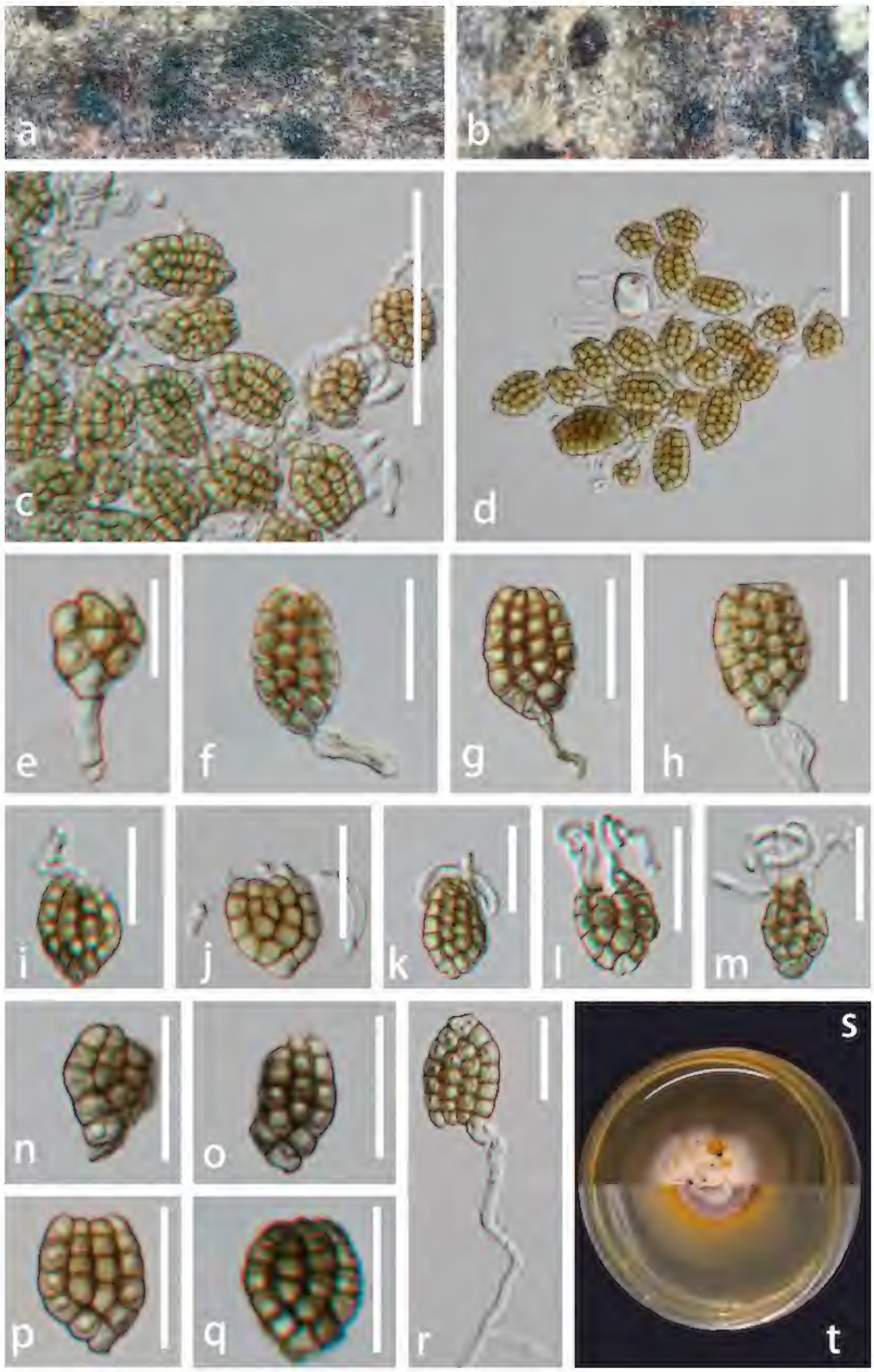

Figure 5. *Dictyosporium phellodendri* (HKAS 149888, holotype). **a, b.** Colonies on the natural substrate; **c, d.** Squash mount of a sporodochium; **e–h.** Conidia with conidiophores; **i–m.** Conidia with appendages; **n–q.** Conidia at different stages; **r.** Germinated conidium; **s, t.** Surface and reverse view of colonies on PDA after 39 days of incubation at 25 °C. Scale bars: 50 μm (**c, d**); 10 μm (**e**); 20 μm (**f–m**); 10 μm (**n**); 20 μm (**o–r**).

3–5 µm wide, micronematous, simple, aseptate, cylindrical, hyaline to pale brown, thin-walled. ***Conidiogenous cells*** 5–8 × 3–6 µm ($\bar{x}$ = 6.3 × 4.7 µm, n = 10), holoblastic, hyaline or pale brown, cylindrical. ***Conidia*** 17–44 × 15–27 µm ($\bar{x}$ = 30 × 21 µm, n = 30), acrogenous, cheiroid, complanate, smooth-walled, pale brown or pale yellow, mostly consisting of four closely adpressed rows of cells, rarely with three or five rows, 33–38 ×4–6 µm ($\bar{x}$ = 35.5 × 5.5 µm, n = 30), 4–10-euseptate in each row, with hyaline, tubular, elongated apical appendages arising from two outer rows, 13–58 × 3–6 µm ($\bar{x}$ = 32.9 × 4.2 µm, n = 15).

Culture characteristics. Conidia produce germ tubes on PDA within 18 hours of incubation at 25 °C. Colonies on PDA are circular, with a flat surface and entire edge, reaching a diameter about 28 mm after 39 days of incubation at 25 °C. The colony appears white on the top view, while the reverse side with pale grey centre and yellow edge.

Material examined. CHINA • Guizhou Province, Guiyang City, Anshun City, Xixiu District, Yaowang Valley, 26°16'17"N, 106°7'0"E, on the rotting branch of *Phellodendron amurense*, 15 October 2024, Shi-Ping Zou, HBYWGC13 (HKAS 149888, holotype), ex-type culture GZCC 25-0522 • *Ibid*., HBYWGC25 (149889), living culture GZCC 25-0523.

Notes. In the phylogenetic analysis, *Dictyosporium phellodendri* (GZCC 25-0522 and GZCC 25-0523) formed a sister clade to *D. muriformis* with 80% ML/0.98PP (Fig. 2), but *D. muriformis*, possesses smaller conidia (20–30 × 11–14.5 µm vs. 26–32 × 15–25 µm), darker pigmentation (median brown vs. pale brown or pale yellow) and the absence of appendages (Hyde et al. 2020). Morphologically, *D. phellodendri* is most similar to *D. alatum* (ATCC 34953) in conidial shape. However, it is distinguished by its larger conidia (17–44 × 15–27 µm vs. 26–32 × 15–25 µm), paler colouration and 4–10 septa per row (Van Emden 1975). Furthermore, comparisons of sequences between *D. phellodendri* and *D. alatum* (ATCC 34953) revealed differences in the ITS region of 13% (64/507 bp, including 11 gaps) and in the LSU region of 3% (18/573 bp, with 4 gaps). We, therefore, designated our collections as a new species, based on morphological and phylogenetic evidence.

Discussion

In this study, three saprobic fungal taxa were collected from terrestrial habitats in Guizhou Province, China. Based on multigene phylogenetic analyses combined with morphological comparative evidence, *Helicosporium phellodendri* and *Dictyosporium phellodendri* are proposed as two novel species, while *Neohelicomyces guizhouensis* is identified as a new host record.

The family Tubeufiaceae (Tubeufiales, Dothideomycetes, Ascomycota) represents an important lineage of helicosporous fungi. Most genera and species in the family exhibit distinct asexual morphs, characterised by filamentous, helicoid (spirally coiled) conidia, which are key diagnostic features for species identification (Barr 1979). To date, 33 *Helicosporium* species, including the new species introduced herein, have been recognised (Bai et al. 2025), while 30 species of *Neohelicomyces* have been accepted (Ma et al. 2025). Members of both genera are commonly isolated from decaying wood or plant litter of unidentified hosts in freshwater and terrestrial habitats (Peng et al. 2025; Sun et al. 2025). Most known species are represented only by their asexual morphs; to date, four species of

Helicosporium and one of *Neohelicomyces* have been reported in their sexual morphs (Brahmanage et al. 2017; Xiao et al. 2023; Sun et al. 2025).

Dictyosporium species play a crucial ecological role as decomposers of decaying wood and plant litter and are reported worldwide from both terrestrial and aquatic environments (Dubey 2022). Ho et al. (2002) investigated the seasonality and succession of fungi on submerged wood and found that *Dictyosporium* species occurred on diverse woody substrates in Tai Po Kau Forest Stream. Furthermore, *Dictyosporium* has been shown to enhance plant growth and resistance to pathogen infection (Peitl et al. 2020; Jiang et al. 2023). *Dictyosporium phellodendri*, isolated from decay branch of *Phellodendron amurense*, suggests that this fungal community plays a functional role in wood decomposition of *Phellodendron amurense* in the ecosystem. Future research may reveal that species of this genus participate in a broader range of ecological functions.

The members of Tubeufiaceae, especially helicosporous taxa, are known to produce diverse bioactive secondary metabolites (Lu et al. 2018b; Ma et al. 2024b). Likewise, *Dictyosporium* species has been recognised as sources of novel natural products (Tran et al. 2019, 2020). All strains isolated in this study originated from the dead branches of *P. amurense*, a medicinal plant rich in bioactive compounds, such as berberine, polyphenols, fibre, phytosterols and carotenoids. Extracts of this plant exhibit a wide range of pharmacological properties, including anti-inflammatory, antibacterial and anticancer activities and are used in the treatment of pneumonia, diarrhoea and circulatory disorders (Kim et al. 2011; Steinmann et al. 2012; Velmurugan et al. 2017; Wang et al. 2017; Sun et al. 2019; Balážová et al. 2022; Erhan et al. 2023; Feng et al. 2023). The isolation of these saprobic fungi from *P. amurense* not only expands our understanding of their biodiversity, but also provides valuable resources for exploring novel bioactive metabolites and elucidating the ecological interactions between fungi and medicinal host plants.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Morphological data, photo-plates and phylogenetic analyses were completed by Shi-Ping Zou, Qiu-Yuan Tang and Yu-Bi Chen. The original draft was written by Shi-Ping Zou. Yuan-Pin Xiao, Ning-Guo Liu, Dan-Feng Bao and Yong-Zhong Lu and Ratchadawan Cheewangkoon revised the paper.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Bai S, Wang F, Wan SR, Lv XK, Chen LJ, Wu R, Ma J (2025) Two novel *Helicosporium* species (Tubeufiaceae, Tubeufiales) from southern China based on morphological and molecular evidence. MycoKeys 124: 159–176. https://doi.org/10.3897/mycokeys.124.168933

Barr ME (1979) A classification of Loculoascomycetes. Mycologia 71(5): 935–957. https://doi.org/10.1080/00275514.1979.12021099

Barr ME (1980) On the family Tubeufiaceae (Pleosporales). Mycotaxon 12(1): 137–167. https://doi.org/10.5962/p.417317

Boonmee S, Zhang Y, Chomnunti P, Chukeatirote E, Tsui CKM, Bahkali AH, Hyde KD (2011) Revision of lignicolous Tubeufiaceae based on morphological reexamination and phylogenetic analysis. Fungal Diversity 51(1): 63–102. https://doi.org/10.1007/s13225-011-0147-4

Boonmee S, Rossman AY, Liu JK, Li WJ, Dai DQ, Bhat JD, Jones EBG, McKenzie EHC, Xu JC, Hyde KD (2014) Tubeufiales, ord. nov., integrating sexual and asexual generic names. Fungal Diversity 68(1): 239–298. https://doi.org/10.1007/s13225-014-0304-7

Boonmee S, D'souza MJ, Luo ZL, Pinruan U, Tanaka K, Su H, Bhat DJ, McKenzie EHC, Jones EBG, Taylor JE, Phillips AJL, Hirayama K, Eungwanichayapant PD, Hyde KD (2016) Dictyosporiaceae fam. nov. Fungal Diversity 80(1): 457–482. https://doi.org/10.1007/s13225-016-0363-z

Boonmee S, Wanasinghe DN, Calabon MS, Huanraluek N, Chandrasiri SK, Jones GE, Rossi W, Leonardi M, Singh SK, Rana S, Singh PN, Maurya DK, Lagashetti AC, Choudhary D, Dai YC, Zhao CL, Mu YH, Yuan HS, He SH, Phookamsak R, Jiang HB, Martín MP,

Dueñas M, Telleria MT, Kałucka IL, Jagodziński AM, Liimatainen K, Pereira DS, Phillips AJL, Suwannarach N, Kumla J, Khuna S, Lumyong S, Potter TB, Shivas RG, Sparks AH, Vaghefi N, Abdel-Wahab MA, Abdel-Aziz FA, Li GJ, Lin WF, Singh U, Bhatt RP, Lee HB, Nguyen TTT, Kirk PM, Dutta AK, Acharya K, Sarma VV, Niranjan M, Rajeshkumar KC, Ashtekar N, Lad S, Wijayawardene NN, Bhat JD, Xu RJ, Wijesinghe SN, Shen HW, Luo ZL, Zhang JY, Sysouphanthong P, Thongklang N, Bao DF, Aluthmuhandiram JVS, Abdollahzadeh J, Javadi A, Dovana F, Usman M, Khalid AN, Dissanayake AJ, Telagathoti A, Probst M, Peintner U, Garrido-Benavent I, Bóna L, Merényi Z, Boros L, Zoltán B, Stielow JB, Jiang N, Tian CM, Shams E, Dehghanizadeh F, Pordel A, Javan-Nikkhah M, Denchev TT, Denchev CM, Kemler M, Begerow D, Deng CY, Harrower E, Bozorov T, Kholmuradova T, Gafforov Y, Abdurazakov A, Xu JC, Mortimer PE, Ren GC, Jeewon R, Maharachchikumbura SSN, Phukhamsakda C, Mapook A, Hyde KD (2021) Fungal diversity notes 1387–1511: Taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 111(1): 1–335. https://doi.org/10.1007/s13225-021-00489-3

Brahamanage RS, Lu YZ, Bhat DJ, Wanasinghe DN, Yan JY, Hyde KD, Boonmee S (2017) Phylogenetic investigations on freshwater fungi in Tubeufiaceae (Tubeufiales) reveals the new genus *Dictyospora* and new species *Chlamydotubeufia aquatica* and *Helicosporium flavum*. Mycosphere: Journal of Fungal Biology 8(7): 917–933. https://doi.org/10.5943/mycosphere/8/7/8

Calado MDL, Carvalho L, Pang KL, Barata M (2015) Diversity and ecological characterization of sporulating higher filamentous marine fungi associated with *Spartina maritima* (Curtis) Fernald in two Portuguese salt marshes. Microbial Ecology 70(3): 612–633. https://doi.org/10.1007/s00248-015-0600-0

Cao FX, Qi PK (1990) The identification of fungal diseases in *Phellodendron amurense*. Journal of Central-South Forestry College 10(1): 40–43.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics (Oxford, England) 25(15): 1972–1973. https://doi.org/10.1093/bioinformatics/btp348

Chaiwan N, Lu YZ, Tibpromma S, Bhat DJ, Hyde KD, Boonmee S (2017) *Neotubeufia* gen. nov. and *Tubeufia guangxiensis* sp. nov. (Tubeufiaceae) from freshwater habitats. Mycosphere: Journal of Fungal Biology 8(9): 1443–1456. https://doi.org/10.5943/mycosphere/8/9/9

Chen MY, Wu ZY, Zou YJ, Peng C, Hao YJ, Zhu ZX, Shi XY, Su BM, Ou L, Lai YQ, Jia JW, Xun MJ, Li H, Zhu WX, Feng Z, Yao MC (2024) Phellodendron chinense C.K. Schneid: An in vitro study on its anti-Helicobacter pylori effect. Journal of Ethnopharmacology 333: 118396. https://doi.org/10.1016/j.jep.2024.118396

Chinese Pharmacopoeia Commission (2020) Pharmacopoeia of the People's Republic of China. China Medical Science and Technology Press.

Corda ACJ (1836) Mykologische Beobachtungen. In: Weitenweber WR (Ed.) Beiträge zur Gesammten Natur- und Heilwissenschaften, 1st ed 1: 80–88.

Corda ACJ (1837) *Icones fungorum hucusque cognitorum*, vol. 1. Calve, Prague.

Dong W, Wang B, Hyde KD, McKenzie EHC, Raja HA, Tanaka K, Abdel-Wahab MA, Abdel-Aziz FA, Doilom M, Phookamsak R, Hongsanan S, Wanasinghe DN, Yu XD, Wang GN, Yang H, Yang J, Thambugala KM, Tian Q, Luo ZL, Yang JB, Miller AN, Fournier J, Boonmee S, Hu DM, Nalumpang S, Zhang H (2020) Freshwater Dothideomycetes. Fungal Diversity 105(1): 319–575. https://doi.org/10.1007/s13225-020-00463-5

Du HZ, Lu YH, Cheewangkoon R, Liu JK (2024) Morpho-phylogenetic evidence reveals novel species and new records of *Nigrograna* (Nigrograna ceae) associated with me-

dicinal plants in Southwestern China. MycoKeys 110: 1–28. https://doi.org/10.3897/mycokeys.110.132628

Dubey R (2022) *Dictyosporium matherense* sp. nov.: A new-fangled cheirosporous fungal species described from the Western Ghats of India. Asian Journal of Forestry 6(1): 1–8. https://doi.org/10.13057/asianjfor/r060101

Dulan B, Wang H, Wu Y, Ling L (2022) Famous traditional Mongolian medicine Xieriga-4 (turmeric-4) decoction: A review. Chinese Herbal Medicines 14(3): 385–391. https://doi.org/10.1016/j.chmed.2022.05.002

Erhan SE, Pârvu AE, Ciorîță A, Putri AA, Villagrana Molina AJ, Pârvu M, Moț AC (2023) Chemical composition and anti-inflammatory effect of *Phellodendron amurense* Rupr. stem bark extract. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 51(3): 13306. https://doi.org/10.15835/nbha51313306

Feng Y, Zheng Y, Xin X, Guo Q, Hao Y, Li C, Zhang Q (2023) Study on chemical constituents and fingerprints of *Phellodendron amurense* Rupr. Journal of Separation Science 46(17): 2300151. https://doi.org/10.1002/jssc.202300151

Fu X, Bao DF, Luo ZL, He X, Su HY (2021) Two new species of *Jalapriya* and a new record, *Dictyocheirospora vinaya* from freshwater habitats in China. Biodiversity Data Journal 9: e74295. https://doi.org/10.3897/BDJ.9.e74295

Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Ho WH, Hyde KD, Hodgkiss IJ (2002) Seasonality and sequential occurrence of fungi on wood submerged in Tai Po Kau Forest Stream, Hong Kong. Fungal Diversity 9: 109–125.

Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN, McKenzie EHC, Sarma VV, Lücking R, Boonmee S, Bhat JD, Liu NG, Tennakoon DS, Pem D, Karunarathna A, Jiang SH, Jones GEB, Phillips AJL, Manawasinghe IS, Tibpromma S, Jayasiri SC, Sandamali D, Jayawardena RS, Wijayawardene NN, Ekanayaka AH, Jeewon R, Lu YZ, Phukhamsakda C, Dissanayake AJ, Zeng XY, Luo ZL, Tian Q, Thambugala KM, Dai DQ, Samarakoon MC, Chethana KWT, Ertz D, Doilom M, Liu JK, Pérez Ortega S, Suija A, Senwanna C, Wijesinghe SN, Niranjan M, Zhang SN, Ariyawansa HA, Jiang HB, Zhang JF, Norphanphoun C, de Silva NI, Thiyagaraja V, Zhang H, Bezerra JDP, Miranda González R, Aptroot A, Kashiwadani H, Harishchandra D, Sérusiaux E, Abeywickrama PD, Bao DF, Devadatha B, Wu H, Moon KH, Gueidan C, Schumm F, Bundhun D, Mapook A, Monkai J, Bhunjun CS, Chomnunti P, Suetrong S, Chaiwan N, Dayarathne MC, Yang J, Rathnayaka AR, Xu JC, Zheng J, Liu G, Feng Y, Xie N (2020) Refined families of Dothideomycetes: Orders and families incertae sedis in Dothideomycetes. Fungal Diversity 105(1): 17–318. https://doi.org/10.1007/s13225-020-00462-6

Hsieh SY, Goh TK, Kuo CH (2021) New species and records of *Helicosporium* sensu lato from Taiwan, with a reflection on current generic circumscription. Mycological Progress 20(2): 169–190. https://doi.org/10.1007/s11557-020-01663-8

Hyde KD, Hongsanan S, Jeewon R, Bhat DJ, McKenzie EHC, Jones EBG, Phookamsak R, Ariyawansa HA, Boonmee S, Zhao Q, Abdel-Aziz FA, Abdel-Wahab MA, Banmai S, Chomnunti P, Cui BK, Daranagama DA, Das K, Dayarathne MC, de Silva NI, Dissanayake AJ, Doilom M, Ekanayaka AH, Gibertoni TB, Goes-Neto A, Huang SK, Jayasiri SC, Jayawardena RS, Konta S, Lee HB, Li WJ, Lin CG, Liu JK, Lu YZ, Luo ZL, Manawasinghe IS, Manimohan P, Mapook A, Niskanen T, Norphanphoun C, Papizadeh M, Perera RH, Phukhamsakda C, Richter C, Santiago ALCMDA, Ricardo Drechsler-Santos E, Senanayake IC, Tanaka K, Tennakoon TMDS, Thambugala KM, Tian Q, Tibpromma S, Thongbai B, Vizzini A, Wanasinghe DN, Wijayawardene N, Wu HX, Yang J, Zeng XY, Zhang

H, Zhang JF, Bulgakov TS, Camporesi E, Bahkali AH, Amoozegar MA, Araujo-Neta LS, Ammirati JF, Baghela A, Bhatt RP, Bojantchev D, Buyck B, da Silva GA, Ferreira de Lima CL, Vilela de Oliveira RJ, Fragoso de Souza CA, Dai YC, Dima B, Duong TT, Ercole E, Mafalda-Freire F, Ghosh A, Hashimoto A, Kamolhan S, Kang JC, Karunarathna SC, Kirk PM, Kytövuori I, Lantieri A, Liimatainen K, Liu ZY, Liu XZ, Lücking R, Medardi G, Mortimer PE, Thi Thuong Thuong Nguyen, Promputtha I, Raj KNA, Reck MA, Lumyong S, Shahzadeh-Fazeli SA, Stadler M, Soudi MR, Su HY, Takahashi T, Tangthirasunun N, Uniyal P, Wang Y, Wen TC, Xu JC, Zhang ZK, Zhao YC, Zhou JL, Zhu L (2016) Fungal diversity notes 367–490: Taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 80: 1–270. https://doi.org/10.1007/s13225-016-0373-x

Hyde KD, Norphanphoun C, Abreu VP, Bazzicalupo A, Thilini Chethana KW, Clericuzio M, Dayarathne MC, Dissanayake AJ, Ekanayaka AH, He MQ, Hongsanan S, Huang SK, Jayasiri SC, Jayawardena RS, Karunarathna A, Konta S, Kušan I, Lee H, Li J, Lin CG, Liu NG, Lu YZ, Luo ZL, Manawasinghe IS, Mapook A, Perera RH, Phookamsak R, Phukhamsakda C, Siedlecki I, Soares AM, Tennakoon DS, Tian Q, Tibpromma S, Wanasinghe DN, Xiao YP, Yang J, Zeng XY, Abdel-Aziz FA, Li WJ, Senanayake IC, Shang QJ, Daranagama DA, de Silva NI, Thambugala KM, Abdel-Wahab MA, Bahkali AH, Berbee ML, Boonmee S, Bhat DJ, Bulgakov TS, Buyck B, Camporesi E, Castañeda-Ruiz RF, Chomnunti P, Doilom M, Dovana F, Gibertoni TB, Jadan M, Jeewon R, Jones EBG, Kang JC, Karunarathna SC, Lim YW, Liu JK, Liu ZY, Plautz Jr HL, Lumyong S, Maharachchikumbura SSN, Matočec N, McKenzie EHC, Mešić A, Miller D, Pawłowska J, Pereira OL, Promputtha I, Romero AI, Ryvarden L, Su HY, Suetrong S, Tkalčec Z, Vizzini A, Wen TC, Wisitrassameewong K, Wrzosek M, Xu JC, Zhao Q, Zhao RL, Mortimer PE (2017) Fungal diversity notes 603–708: Taxonomic and phylogenetic notes on genera and species. Fungal Diversity 87(1): 1–235. https://doi.org/10.1007/s13225-017-0391-3

Hyde KD, Dong Y, Phookamsak R, Jeewon R, Bhat DJ, Jones EG, Liu NG, Abeywickrama PD, Mapook A, Wei D, Perera RH, Manawasinghe IS, Pem D, Bundhun D, Karunarathna A, Ekanayaka AH, Bao DF, Li J, Samarakoon MC, Chaiwan N, Lin CG, Phutthacharoen K, Zhang SN, Senanayake IC, Goonasekara ID, Thambugala KM, Phukhamsakda C, Tennakoon DS, Jiang HB, Yang J, Zeng M, Huanraluek N, Liu JK, Wijesinghe SN, Tian Q, Tibpromma S, Brahmanage RS, Boonmee S, Huang SK, Thiyagaraja V, Lu YZ, Jayawardena RS, Dong W, Yang EF, Singh SK, Singh SM, Rana S, Lad SS, Anand G, Devadatha B, Niranjan M, Sarma VV, Liimatainen K, Aguirre-Hudson B, Niskanen T, Overall A, Alvarenga RLM, Gibertoni TB, Pfliegler WP, Horváth E, Imre A, Alves AL, Silva Santos AC, Vieira Tiago P, Bulgakov TS, Wanasinghe DN, Bahkali AH, Doilom M, Elgorban AM, Maharachchikumbura SSN, Rajeshkumar CC, Haelewaters D, Mortimer PE, Zhao Q, Lumyong S, Xu J, Sheng J (2020) Fungal diversity notes 1151–1276: Taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 100(1): 5–277. https://doi.org/10.1007/s13225-020-00439-5

Index Fungorum (2025) Index Fungorum. https://www.speciesfungorum.org/

Jiang SH, Jones GEB, Phillips AJL, Manawasinghe IS, Tibpromma S, Jayasiri SC, Jiang Y, Liu J, Liang S, Zhu W, Li H (2023) Changes in phyllosphere microbial communities of *Pinus tabuliformis* after infestation by *Bursaphelenchus xylophilus*. Forests 14(2): 179. https://doi.org/10.3390/f14020179

Karimi O, Hyde KD, Asghari R, Chethana KWT, Kaewchai S, Al-Otibi F, Li QR (2025) Peat swamp Ascomycota associated with palms (Arecaceae) from Narathiwat, Thailand. Mycosphere: Journal of Fungal Biology 16(1): 2456–2575. https://doi.org/10.5943/mycosphere/16/1/14

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Kim JH, Huh JE, Baek YH, Lee JD, Choi DY, Park DS (2011) Effect of *Phellodendron amurense* in protecting human osteoarthritic cartilage and chondrocytes. Journal of Ethnopharmacology 134(2): 234–242. https://doi.org/10.1016/j.jep.2010.12.005

Kirk PM, Cannon PF, David JC, Stalpers JA (2001) Ainsworth & Bisby's Dictionary of the Fungi, 9th edn. CABI, Wallingford.

Kodsueb R, Jeewon R, Vijaykrishna D, McKenzie EHC, Lumyong P, Lumyong S, Hyde KD (2006) Systematic revision of Tubeufiaceae based on morphological and molecular data. Fungal Diversity 21: 105–130.

Li D (2006) Preliminary study on bioactive component-producing endophytic fungi in the vulnerable medicinal plant *Phellodendron amurense*. M.Sc. Thesis, Northwest University, Xi'an, China.

Li D, Guo LW, Yin H, Feng HG, Li YL (2009) Isolation and characterization of berberine-producing endophytic fungi in *Phellodendron amurense*. Anhui Agricultural Sciences 37(22): 10340–10341, 10350. https://doi.org/10.13989/j.cnki.0517-6611.2009.22.096

Li SJ, Cui YT, Fang XM, He QQ, Zhu TH, Qiao TM, Han S (2018) First report of *Nectria haematococca* as the causal agent of canker rot in *Phellodendron amurense* in China. Plant Disease 102(5): 1033. https://doi.org/10.1094/PDIS-10-17-1542-PDN

Linder DH (1929) A monograph of the helicosporous fungi imperfecti. Annals of the Missouri Botanical Garden 16(3): 227–388. https://doi.org/10.2307/2394038

Link HF (1809) Observationes in ordines plantarum naturales. Dissertatio I. Mag Ges Naturf Freunde Berlin 3: 3–42.

Liu YJ, Whelen S, Hall BD (1999) Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerse II subunit. Molecular Biology and Evolution 16(12): 1799–1808. https://doi.org/10.1093/oxfordjournals.molbev.a026092

Liu JK, Lu YZ, Cheewangkoon R, To-Anun C (2018) Phylogeny and morphology of *Helicotubeufia* gen. nov., with three new species in Tubeufiaceae from aquatic habitats. Mycosphere: Journal of Fungal Biology 9(3): 495–509. https://doi.org/10.5943/mycosphere/9/3/4

Liu F, Bonthond G, Groenewald JZ, Cai L, Crous PW (2019a) Sporocadaceae, a family of coelomycetous fungi with appendage-bearing conidia. Studies in Mycology 92(1): 287–415. https://doi.org/10.1016/j.simyco.2018.11.001

Liu F, Wang J, Li H, Wang W, Cai L (2019b) *Setophoma* spp. on *Camellia sinensis*. Fungal Systematics and Evolution 4: 43–57. https://doi.org/10.3114/fuse.2019.04.05

Liu LN, Mou GF, Bau T (2019c) A new *Gerronema* species with striking colours from China. Phytotaxa 405: 074–082. https://doi.org/10.11646/phytotaxa.405.2.2

Liu NG, Lu YZ, Bhat DJ, McKenzie EHC, Lumyong S, Jumpathong J, Liu JK (2019) *Kevinhydea brevistipitata* gen. et sp. nov. and *Helicoma hydei* sp. nov. (Tubeufiaceae) from decaying wood habitats. Mycological Progress 18: 671–682. https://doi.org/10.1007/s11557-019-01480-8

Lu YZ, Boonmee S, Bhat DJ, Hyde KD, Kang JC (2017a) *Helicosporium luteosporum* sp.nov. and *Acanthohelicospora aurea* (Tubeufiaceae, Tubeufiales) from terrestrial habitats. Phytotaxa 319(3): 241–253. https://doi.org/10.11646/phytotaxa.319.3.3

Lu YZ, Boonmee S, Dai DQ, Liu JK, Hyde KD, Bhat DJ, Kang JC (2017b) Four new species of *Tubeufia* (Tubeufiaceae, Tubeufiales) from Thailand. Mycological Progress 16(4): 403–417. https://doi.org/10.1007/s11557-017-1280-6

Lu YZ, Boonmee S, Liu JK, Hyde KD, Bhat DJ, Eungwanichayapant PD, Kang JC (2017c) Novel *Neoacanthostigma* species from aquatic habitats. Cryptogamie. Mycologie 38(2): 169–190. https://doi.org/10.7872/crym/v38.iss2.2017.169

Lu YZ, Boonmee S, Liu JK, Hyde KD, McKenzie EHC, Eungwanichayapant PD, Kang JC (2018a) Multi-gene phylogenetic analyses reveals *Neohelicosporium* gen. nov. and five new species of helicosporous hyphomycetes from aquatic habitats. Mycological Progress 17(5): 631–646. https://doi.org/10.1007/s11557-017-1366-1

Lu YZ, Liu JK, Hyde KD, Jeewon R, Kang JC, Fan C, Boonmee S, Bhat DJ, Luo ZL, Lin CG, Eungwanichayapant PD (2018b) A taxonomic reassessment of Tubeufiales based on multi-locus phylogeny and morphology. Fungal Diversity 92(1): 131–344. https://doi.org/10.1007/s13225-018-0411-y

Lu YZ, Ma J, Xiao XJ, Zhang LJ, Xiao YP, Kang JC (2022) Four new species and three new records of helicosporous hyphomycetes from China and their multi-gene phylogenies. Frontiers in Microbiology 13: 1053849. https://doi.org/10.3389/fmicb.2022.1053849

Lumbsch HT, Huhndorf SM (2010) Outline of Ascomycota 2009. Myconet 14: 1–64. https://doi.org/10.3158/1557.1

Luo ZL, Bhat DJ, Jeewon R, Boonmee S, Bao DF, Zhao YC, Chai HM, Su HY, Su XJ, Hyde KD (2017) Molecular phylogeny and morphological characterization of asexual fungi (Tubeufiaceae) from freshwater habitats in Yunnan, China. Cryptogam Mycol 38(1): 27–53. https://doi.org/10.7872/crym/v38.iss1.2017.27

Ma J, Gomdola D, Boonmee S, Shen HW, Tang X, Lu YZ, Hyde KD (2024a) Three new species of *Neohelicomyces* (Tubeufiales, Tubeufiaceae) from freshwater and terrestrial habitats in China. MycoKeys 105: 317–336. https://doi.org/10.3897/mycokeys.105.124129

Ma J, Hyde KD, Tibpromma S, Karunarathna SC, Gomdola D, Norphanphoun C, Liu NG, Bao DF, Boonmee S, Xiao XJ, Zhang LJ, Luo ZL, Zhao Q, Liu JK, Lu YZ (2024b) Taxonomy and systematics of lignicolous helicosporous hyphomycetes. Fungal Diversity 129(1): 365–653. https://doi.org/10.1007/s13225-024-00544-9

Ma XY, Song DD, Ma J (2025) Morphological and phylogenetic analyses reveal two new species of *Neohelicomyces* (Tubeufiales, Tubeufiaceae) from China. MycoKeys 121: 237–251. https://doi.org/10.3897/mycokeys.121.158721

Morgan-Jones G, Goos R (1992) *Chloridium virescens* and *Helicosporium virescens*, binominals for different fungi based on the same basionym *Dematium virescens*. Mycologia 84(6): 921–923. https://doi.org/10.1080/00275514.1992.12026226

Nees Von Esenbeck CDG (1817) System der Pilze und Schwämme; Wentworth Press, Würtzburg, Germany, 1–334. https://doi.org/10.5962/bhl.title.110007

Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Nylander JAA, Zoology S, Posada D, Mrmodeltest R, Os F (2008) MrModeltest2 v. 2.3 (Program for Selecting DNA Substitution Models Using PAUP*). Evolutionary Biology Centre: Uppsala, Sweden.

Peitl DC, Sumida CH, Gonçalves RM, Pascholati SF, Balbi-Peña MI (2020) Antagonism of saprobe fungi from semiarid areas of the Northeast of Brazil against *Sclerotinia sclerotiorum* and biocontrol of soybean white mold. Semina. Ciências Agrárias 41(6): 2597–2612. https://doi.org/10.5433/1679-0359.2020v41n6p2597

Peng T, Lu YZ, Bai S, Zhang JY, Xiao XJ, Wu N, Ma J (2025) Novel *Helicosporium* and *Neohelicomyces* (Tubeufiaceae, Tubeufiales) species from terrestrial habitats in China and Thailand. MycoKeys 112: 81–101. https://doi.org/10.3897/mycokeys.112.140211

Rehner SA, Buckley E (2005) A beauveria phylogeny inferred from nuclear ITS and EF1-α sequences: Evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97(1): 84–98. https://doi.org/10.3852/mycologia.97.1.84

Rossman AY (1987) The Tubeufiaceae and similar Loculoascomycetes. Mycological Papers 157: 1–71.

Samuels GJ, Müller E (1979) Life-history studies of Brazilian Ascomycetes. 2. A new species of *Thaxteriella* and its helicosporous anamorph. Sydowia. Annales Mycologici 32(1–6): 294–302.

Senanayake IC, Rathnayaka AR, Marasinghe DS, Calabon MS, Gentekaki E, Lee HB, Hurdeal VG, Pem D, Dissanayake LS, Wijesinghe SN, Bundhun D, Nguyen TT, Goonasekara ID, Abeywickrama PD, Bhunjun CS, Jayawardena RS, Wanasinghe DN, Jeewon R, Bhat DJ, Xiang MM (2020) Morphological approaches in studying fungi: Collection, examination, isolation, sporulation and preservation. Mycosphere: Journal of Fungal Biology 11(1): 2678–2754. https://doi.org/10.5943/mycosphere/11/1/20

Shen HW, Bao DF, Wanasinghe DN, Boonmee S, Liu JK, Luo ZL (2022) Novel species and records of Dictyosporiaceae from freshwater habitats in China and Thailand. Journal of Fungi (Basel, Switzerland) 8(11): 1200. https://doi.org/10.3390/jof8111200

Spatafora JW, Sung GH, Johnson D, Hesse C, O'Rourke B, Serdani M, Spotts R, Lutzoni F, Hofstetter V, Miadlikowska J, Reeb V, Gueidan C, Fraker E, Lumbsch T, Lücking R, Schmitt I, Hosaka K, Aptroot A, Roux C, Miller AN, Geiser DM, Hafellner J, Hestmark G, Arnold AE, Büdel B, Rauhut A, Hewitt D, Untereiner WA, Cole MS, Scheidegger C, Schultz M, Sipman H, Schoch CL (2006) A five-gene phylogeny of Pezizomycotina. Mycologia 98(6): 1018–1028. https://doi.org/10.1080/15572536.2006.11832630

Steinmann D, Baumgartner RR, Heiss EH, Bartenstein S, Atanasov AG, Dirsch VM, Ganzera M, Stuppner H (2012) Bioguided isolation of (9Z)-octadec-9-enoic acid from *Phellodendron amurense* Rupr. and identification of fatty acids as PTP1B inhibitors. Planta Medica 78(3): 219–224. https://doi.org/10.1055/s-0031-1280377

Sun Y, Lenon GB, Yang AWH (2019) Phellodendri Cortex: A phytochemical, pharmacological, and pharmacokinetic review. Evidence-Based Complementary and Alternative Medicine : eCAM 7621929: 1–45. https://doi.org/10.1155/2019/7621929

Sun YR, Hyde KD, Liu NG, Jayawardena RS, Wijayawardene NN, Ma J, Zhang Q, Al-Otibi F, Wang Y (2025) Micro-fungi in southern China and northern Thailand: Emphasis on medicinal plants. Fungal Diversity 131(1): 99–299. https://doi.org/10.1007/s13225-024-00549-4

Swindell SR, Plasterer TN (1997) Seqman. Sequence data analysis guidebook. Springer, 75–89. https://doi.org/10.1385/0-89603-358-9:75

Tran TD, Wilson BA, Henrich CJ, Staudt LM, Krumpe LR, Smith EA, Gustafson KR (2019) Secondary metabolites from the fungus *Dictyosporium* sp. and their MALT1 inhibitory activities. Journal of Natural Products 82(1): 154–162. https://doi.org/10.1021/acs.jnatprod.8b00871

Tran TD, Wilson BA, Henrich CJ, Wendt KL, King J, Cichewicz RH, Gustafson KR (2020) Structure elucidation and absolute configuration of metabolites from the soil-derived fungus *Dictyosporium digitatum* using spectroscopic and computational methods. Phytochemistry 173: 112278. https://doi.org/10.1016/j.phytochem.2020.112278

Tsui CKM, Sivichai S, Berbee ML (2006) Molecular systematics of *Helicoma*, *Helicomyces* and *Helicosporium* and their teleomorphs inferred from rDNA sequences. Mycologia 98(1): 94–104. https://doi.org/10.1080/15572536.2006.11832715

Vaidya G, Lohman DJ, Meier R (2011) SequenceMatrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cla-

distics: The International Journal of the Willi Hennig Society 27(2): 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

Van Emden JH (1975) Three new fungi from Surinam soil. Acta Botanica Neerlandica 24(2): 193–197. https://doi.org/10.1111/j.1438-8677.1975.tb01006.x

Velmurugan N, Kalpana D, Cho JY, Lee YS (2017) Chemical composition and antioxidant capacity of the aqueous extract of *Phellodendron amurense*. Journal of Forestry Research 29(4): 1041–1048. https://doi.org/10.1007/s11676-017-0532-2

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8): 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Wang L, Wang X, Zhu XM, Liu YQ, Du WJ, Ji J, He X, Zhang CF, Li F, Guo CR (2017) Gastroprotective effect of alkaloids from Cortex Phellodendri on gastric ulcers in rats through neurohumoral regulation. Planta Medica 83: 277–284. https://doi.org/10.1055/s-0042-114044

Wang WC, Li QY, Liu YH, Chen BB (2015) Ionic liquid-aqueous solution ultrasonic-assisted extraction of three kinds of alkaloids from *Phellodendron amurense* Rupr and optimization of conditions using response surface methodology. Ultrasonics Sonochemistry 24: 13–18. https://doi.org/10.1016/j.ultsonch.2014.10.009

Wang Y, Bhat DJ, Bao D-F, Shen H-W, Feng Y, Luo Z-L (2025) Morpho-molecular analyses reveal two novel species and two new records of Dictyosporiaceae (Pleosporales) from Dulongjiang River in northwestern Yunnan Province, China. MycoKeys 117: 1–27. https://doi.org/10.3897/mycokeys.117.145587

Wen J, Okyere SK, Wang S, Wang J, Xie L, Ran Y, Hu Y (2022) Endophytic fungi: An effective alternative source of plant-derived bioactive compounds for pharmacological studies. Journal of Fungi (Basel, Switzerland) 8(2): 205. https://doi.org/10.3390/jof8020205

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR protocols: a guide to methods and applications, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wijayawardene NN, Hyde KD, Dai DQ, Sanchez-Garcia M, Goto BT, Saxena RK, Erdoğdu M, Selcuk F, Rajeshkumar KC, Aptroot A, Błaszkowski J, Boonyuen N, da Silva GA, de Souza FA, Dong W4, Ertz D, Haelewaters D, Jones EBG, Karunarathna SC, Kirk PM, Kukwa M, Kumla J, Leontyev DV, Lumbsch HT, Maharachchikumbura SSN, Marguno F, Martinez-Rodriguez P, Mešić A, Monteiro JS, Oehl F, Pawłowska J, Pem D, Pfliegler WP, Phillips AJL, Pošta A, He MQ, Li JX, Raza M, Sruthi OP, Suetrong S, Suwannarach N, Tedersoo L, Thiyagaraja V, Tibpromma S, Tkalčec Z, Tokarev YS, Wanasinghe DN, Wijesundara DSA, Wimalaseana SDMK, Madrid H, Zhang GQ, Gao Y, Sanchez-Castro I, Tang LZ, Stadler M, Yurkov A, Thines M (2022) Outline of Fungi and fungus-like taxa – 2021. Mycosphere13: 53–453. https://doi.org/10.5943/mycosphere/13/1/2

Xian X, Sun B, Ye X, Zhang G, Hou P, Gao H (2014) Identification and analysis of alkaloids in cortex *Phellodendron amurense* by high-performance liquid chromatography with electrospray ionization mass spectrometry coupled with photodiode array detection. Journal of Separation Science 37(13): 1533–1545. https://doi.org/10.1002/jssc.201400012

Xiao XJ, Ma J, Zhang LJ, Liu NG, Xiao YP, Tian XG, Luo ZL, Lu YZ (2023) Additions to the Genus *Helicosporium* (Tubeufiaceae, Tubeufiales) from China with an Identification Key to *Helicosporium* Taxa. Journal of Fungi (Basel, Switzerland) 2023(9): 775. https://doi.org/10.3390/jof9070775

Yang J, Liu JK, Hyde KD, Jones EBG, Liu ZY (2018) New species in *Dictyosporium*, new combinations in *Dictyocheirospora* and an updated backbone tree for Dictyosporiaceae. MycoKeys 36: 83–105. https://doi.org/10.3897/mycokeys.36.27051

Yang J, Liu LL, Jones EBG, Hyde KD, Liu ZY, Bao DF, Liu NG, Li WL, Shen HW, Yu XD, Liu JK (2023) Freshwater fungi from karst landscapes in China and Thailand. Fungal Diversity 119(1): 1–212. https://doi.org/10.1007/s13225-023-00514-7

Zeng XY, Tan TJ, Tian FH, Wang Y, Wen TC (2023) OFPT: A one-stop software for fungal phylogeny. Mycosphere: Journal of Fungal Biology 14(1): 1730–1741. https://doi.org/10.5943/mycosphere/14/1/20

Zhang W, Li X, Wang Y (2020) Ecological distribution and morphological characteristics of Tubeufiaceae species in tropical regions. Fungal Ecology 50: 42–50.

Zhang JF, Liu JK, Hyde KD, Chen YY, Ran HY, Liu ZY (2023) Ascomycetes from karst landscapes of Guizhou Province, China. Fungal Diversity 122(1): 1–160. https://doi.org/10.1007/s13225-023-00524-5

Zhang WR, Gao RR, Tian LX, Xu ZC (2024) Integrated microbiome and metabolomics analysis reveal the relationship between plant-specialized metabolites and microbial community in *Phellodendron amurense*. Frontiers in Plant Science 15: 1363063. https://doi.org/10.3389/fpls.2024.1363063

Zhao GZ, Liu XZ, Wu WP (2007) Helicosporous hyphomycetes from China. Fungal Diversity 26: 313–524.